

# THE ANNALS

AND

## MAGAZINE OF NATURAL HISTORY.

[SIXTH SERIES.]

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"..... per litora spargite muscum,  
Naiades, et circum vitreos considite fontes:  
Pollice virgineo teneros hic carpite flores:  
Floribus et pictum, divæ, replete canistrum.  
At vos, o Nymphæ Craterides, ite sub undas;  
Ite, recurvato variata corallia trunco  
Vellite muscosis e rupibus, et mihi conchas  
Ferte, Deæ pelagi, et pingui conchyliis succo."  
*N. Parthenii Giannettasii* Ecl. 1.

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### I.—*Observations on the Origin of Hair and on Scales in Mammals.* By MAX WEBER\*.

No structure is more characteristic of Mammals than the hairy covering. From a physiological standpoint also it is in many respects a very significant organ, and on this head naturalists are generally agreed.

In striking contrast to this conviction is our ignorance as to the origin of this important structure. If we are unwilling to regard hair as an organ *sui generis*, our knowledge as to its phylogeny does not rise above the level of hypotheses.

There are two hypotheses which may be mentioned.

Of these one which has been repeatedly expressed assumes that hair, feathers, and scales are comparable structures, and that the two former have developed from scales or scale-like formations. The latter conclusion is to a certain extent an evident one, in so far as scales are more primitive contrivances on the part of the integument, and are characteristic of the Reptiles, which are inferior to the Birds and Mammals in position.

\* Translated from the 'Anatomischer Anzeiger,' viii. Jahrg., nos. 12 and 13, May 13, 1893, pp. 413-423.

As regards hair this hypothesis is not without opponents, who, however, have attacked it only in so far as it deals with the development of the three structures.

A second hypothesis as to the origin of hair has recently been advanced by Maurer\*. This author finds it quite impossible to emphasize sufficiently the difference that exists between scales, feathers, and hair as regards the manner of their earliest development. He states, however, that a great agreement is found between the earliest rudiments of reptilian scales and feathers, since in both cases the rudiment consists of a papilla of the corium, above which the epidermis at first extends unaltered. A hair, on the other hand, arises, according to Maurer, as an epithelial bud, wherein the corium in the first instance takes no share whatever†, though it soon afterwards does so. Nevertheless he admits that the epithelial rudiment of the hair frequently originates upon the summit of a previously-formed papilla of the corium. He regards, however, "the relation of the hair-rudiment to the corium-papilla as a purely topographical one." Maurer then proceeds to explain why a large cutis-papilla of this kind has nothing to do with the hair-rudiment as such. He states that it never becomes the hair-papilla; the permanent hair-papilla is always a subsequent formation. Since Maurer then goes on to assert that he "ascribes great importance to the primitive cutis-papilla," and that "it is undoubtedly homologous with the primitive feather-papilla and with the primitive

\* 'Morphologisches Jahrbuch,' Bd. xviii. p. 717.

† Maurer, however, even in his earliest stages already figures a co-existent first rudiment of the subsequent connective-tissue hair-follicle. According to this, therefore, the cutis would participate in the formation of the hair just as soon as the epidermis. The following consideration might perhaps have been worthy of mention. The high degree of specialization which hair has attained indicates a long previous history. The specialization was directed towards longitudinal growth, consequently to the production of corneous matter, and therefore to advanced functional capacity of the epithelial portion of the hair. That this finally made itself apparent in the individual development also of the hair by means of precocious participation of the epithelial portion as soon as the first rudiment of the hair was formed, while the connective-tissue portion, on the contrary, underwent a regressive process, appears to me to be a point that at least deserves to be mentioned. It would be conceivable that the recession in point of time also on the part of the papilla, which subsequently becomes the hair-papilla, did not take place until the class of hair-bearing animals ("Haartiere") was reached. It would not be the first instance of the gradual acquisition by a composite organ of an ontogenetic development which no longer harmonizes with its phylogenetic evolution. Since in considering the very important question of the phylogeny of hair it certainly behoves us to be cautious, this point should at least be touched upon.

rudiment of the reptilian scale," we may deduce the following conclusions. In the Mammalian integument primary corium-papillæ may first appear which are homologous with the scales of Reptiles and are of only transitory duration. Upon these secondary but permanent hair-papillæ may develop, though never until the formation of the epithelial hair-bud has taken place. Hair-rudiments may, however, also be formed in the smooth skin.

The epithelial hair-bud is derived by Maurer from nerve-end eminences, as found in Pisces and Amphibia. In very instructive fashion Maurer develops step by step the points in which the two organs agree. Finally he shows how, in the modification of a specific integumentary sense-organ of the Amphibia into a simple sensory dermal organ like hair, a change of function must occur. This was probably ushered in by the loss on the part of the integumentary sense-organ, owing to adaptation to terrestrial life, of its primary sensory nerves (which came from the vagus), and the acquisition of simple sensory branches of spinal nerves. By this means it became a sensory organ of the integument without specific character, and capable of further development into the hair.

A rudimentary Amphibian integumentary sense-organ, evincing a tendency towards the formation of corneous matter, is indeed a long way from a hair; yet the interval can be traversed by the train of thought which sets up the hypothesis.

Greater difficulty is found in arriving at the hairy coat. Maurer's deduction takes the following shape. The aforesaid integumentary sense-organs of Amphibia were originally distributed in connexion with the *ramus lateralis* of the vagus nerve. In old animals "it is possible to demonstrate a multiplication of the organs, a dissolution of the three rows which were originally present. The rows become indistinct. At the same time in the groups of organs an indication of the formation of rows is still demonstrable." Further on we read (p. 795):—"In the arrangement of Mammalian hairs also it is always possible to recognize to a certain extent the formation of rows. I regard these as vestiges of the regular arrangement of the integumentary sense-organs in Amphibia." Upon what this conception is based is not clear. The third term of the comparison must, however, be the manner of the arrangement of the rows of hairs and of the rows of dermal sense-organs. We miss the proof of a similarity in this respect. Of the rows of Amphibian integumentary sense-organs it was merely stated a few lines before that they become indistinct, but that in the groups of organs an indica-

tion of the formation of rows is still demonstrable. And with reference to hairs we read on page 722 that, contrary to feathers which are arranged in constant rows, "they are more uniformly distributed over the entire body; it is true that they sometimes form rows, but these are not referable to the arrangement exhibited by the scales of Reptiles."

It is certainly not my intention to call to account the respected author, who is also responsible for this suggestive investigation, for possible trivial discrepancies. These, however, point to the slight extent and the vagueness of our knowledge as to the arrangement of the hair. And yet this very elementary question plays no unimportant part in the whole matter.

In opposition to Maurer's repeated assertion that the arrangement of hairs is not referable to that of Reptilian scales, I should like to attempt to prove that such may well be the case.

A close investigation \* into the structure and development of the so-called scales of *Manis* taught me, in connexion with the studies made by Leydig †, that they are horny scutes which rest upon an enormous papilla of the cutis. The latter is a bilaterally symmetrical flattened elevation of the derm, which is bent in towards the tail, and upon which a dorsal and a ventral surface can accordingly be distinguished. Arranged in imbricated fashion, these scales differ from those of Reptiles only in subordinate points, corresponding to the difference which is inherent in the Reptilian and Mammalian integument as such. In consequence of this it is true that a perfect homology between the scales of *Manis* and those of Reptiles is out of the question; but I certainly thought it possible to conclude that both arose from common ground, and that even the scales of the *Manidæ* are structures which are to be derived from the scales of primitive Reptiles. If this conception is correct, we must expect that elsewhere also among Mammals dermal structures still persist which, without making too long a detour, can be traced back to Reptilian scales. This, too, is actually the case. I found a coat of scales upon the tail of *Anomalurus*, *Myrmecophaga jubata*, *M. tamandua*, *Didelphys*, *Mus*, and *Castor canadensis*. The scales were always—although in different stages of degeneration and modification—constructed according to the same type, as is shown at once by my numerous figures. Hairs

\* Max Weber, 'Zoologische Ergebnisse einer Reise in Niederländ. Ost-Indien,' Leiden, 1892, Bd. ii. p. 5.

† F. Leydig, Müller's 'Archiv für Anatomie und Physiologie,' 1859, p. 704.

are always wanting upon these scales, but they appear behind and sometimes also between them. Where the scales are well developed slight development of the hair is usually noticeable. This is especially striking in the case of so-called naked tails. Naked indeed they are not, *e.g.* the tails of rats and mice, but the quadrangular scales are here arranged in rings. Behind each scale project the hairs, which accordingly assume a verticillate arrangement. In other forms (*Didelphys*, *Myrmecophaga tamandua*) the scales are imbricated and the scanty hairs appear behind them. These different conditions led me to the important conclusion that the scales are the primary structures and that the arrangement of the hairs is due to them. This proposition is literally confirmed by Römer \*, in his recently-published investigations upon the armature of the armadillos. The author referred to found this armature—apart from the ossification which subsequently sets in—to be composed of scales, “to which he attaches the morphological value of a scale in the sense of the scales of Reptiles.”

My earlier investigations led me to conclude that in former times Mammals in general were provided with a coat of scales which in the case of *Manis*, albeit in a peculiarly specialized manner, still extends over the entire body, so far as it is turned towards the light. Elsewhere, on the contrary, I found it still persisting upon the tail alone. This point naturally attracted attention, and to a certain extent the following explanation seemed to suggest itself:—The tail, as a terminal structure of the body which has in many cases not undergone specialization, might have preserved more primitive conditions in its integument than the trunk. For the trunk a thick coat of hair was of importance, if only to preserve the animal heat. A hairy coat of this kind naturally came into conflict with the covering of scales, as to which proofs will be furnished later.

In spite of this, my hypothesis here exhibited its weak side †. Hence it was inevitable that there should arise, to a certain extent of itself, the question whether there are still found in the case of other Mammals, and also in other places, indications of a coat of scales, or at least indications of the previous existence of such a coat.

\* Römer, Jenaische Zeitschr. f. Naturw. Bd. xxvii., 1893, p. 543.

† This was, moreover, not entirely disposed of by the observation made in the meantime by von Jentink (in Max Weber's ‘Zoologische Ergebnisse einer Reise in Niederländ. Ost-Indien,’ Bd. iii. p. 81), that also in the case of mice scales appear upon the extremities,—an observation which was extended by de Meijere (*l. i. c.*) to numerous Rodentia, to Dasypodidae, and especially to Insectivora.



The response to this question must be connected with my observation already mentioned, that the hairs appear behind the scales, never upon them. In consequence of this I came to the conclusion that the hairs are dependent upon the scales in their arrangement. If the scales are imbricated, which was probably the primitive condition, the hairs must consequently form alternating rows and groups. Now what will happen when the scales disappear? Will the hairs preserve their arrangement, as though they still stood behind scales, or will they lose this regular formation? In the event of the first-mentioned case, we might conversely find in it the proof of the former presence of scales. The question to be answered would therefore be, whether in scaleless Mammals, or upon regions of the skin without scales, the hairs are so arranged as though they stood behind scales.

The abundant literature upon the subject of hair supplied no answer upon this point, since beyond incidental observations, with which there was really nothing to be done, it contains nothing that touches the question. Now this problem has been made by Heer J. C. H. de Meijere\* the object of an exhaustive investigation, which was conducted in my laboratory, and will shortly also be made accessible in a German form to a wider circle of interested students. De Meijere examined two hundred and twenty species of Mammals, and arrived at various surprising results, of which the following is the only one that here concerns us. In the great majority of cases the hairs are arranged in alternating groups, which are formed in very different ways. As a primitive and very simple condition must rank a group which consists of three similar hairs†. Usually, however, the hairs in a group are more numerous. At the same time the hairs may issue from isolated follicles or form bundles. De Meijere distinguishes false bundles, which have arisen through fusion of follicles, and genuine bundles. The latter probably arose through the formation upon a follicle of several secondary ones by means of budding. It is an important fact that bundles of this kind also appear in alternating groups. Now if we further consider that upon the scale-bearing portions of the integument the hairs represent alternating groups, and that upon the scaleless portions they frequently form exactly such groups, or that their arrangement is usually traceable thereto,

\* De Meijere, 'Over de haren der Zoogdieren in 't byzonder over hunne wijze van rangschikking,' Dissert. Amsterdam, 1893.

† The important occurrence of three hairs behind scales in mice has already been pointed out by Jentink in the memoir previously quoted (Zoolog. Ergebnisse, iii. p. 81).

we may well assume that the portions of the skin which are now scaleless formerly likewise bore scales. The scales were lost, but the arrangement of the hairs still exhibits their former presence. At any rate, I do not know of any other cause to mention such as would be capable of explaining the regular alternating arrangement.

Through this important result of de Meijere's investigation my hypothesis acquires considerable support, just as conversely it explains and makes intelligible the observations of de Meijere.

Römer, who, in his thankworthy paper, by the investigation of the armature of the armadillos comes to the conclusion that this is likewise composed of scales, conforms entirely to my view with regard to their morphological value. In two points, however, he differs from me. In the first place he considers scales to be a secondary acquisition on the part of Mammals.

It would appear to me that the entire series of de Meijere's results is a continuous argument against this view. The arrangement of the hairs points to the former general existence of a coat of scales. The facts bearing upon this were, however, still unknown when Römer concluded his investigations. But even the facts of the case, as my investigation left them, must plead against the view that the scales have been secondarily acquired; for if so we should have to explain the repeated occurrence of scales as being due to convergence. I am certainly imbued with the importance of the phenomena of convergence in Mammals. I have even so long ago as 1886, in my paper on the origin of the Cetacea, pointed out probably more than my predecessors the importance of this process. But there is a limit in all things.

Römer\* writes (p. 546):—“*Manis* and *Dasypus* are to be derived from true hair-bearing animals, and their present scale-like body-covering is to be regarded as a new acquisition of a secondary nature, which has arisen in consequence of adaptation to the similar burrowing mode of life. . . .” I will pass over the fact that the mode of life of the species of *Manis* is in part very dissimilar from that of the Dasypodidæ. *Manis tricuspis*, Raf., and *M. longicaudata*, Briss., are exclusively arboreal, and *M. javanica*, Desm., partially so. Furthermore, *M. crassicaudata*, St.-Hil., and *M. aurita*, Hodgs., are also climbers; but both are actually capable of digging holes to dwell in. *Manis gigantea*, Ill., and *M. Temminckii*, Smuts, are the only species which are exclusively terrestrial.

\* F. Römer, Jenaische Zeitschrift f. Naturw. Bd. xxvii.

Yet even were the *Manidæ* also burrowers in the sense that the *Dasypodidæ* are, it would certainly be surprising that among the large number of most pronounced burrowers among Marsupials, Insectivores, and Rodents not a single one should have acquired a coat of scales. Further on we read (p. 547):—"As their embryology shows, both originate from true, typical, hair-bearing animals, which in consequence of a newly adopted mode of life have acquired a new body-covering." Much is here demanded of embryology. Yet we find in Römer's paper no new facts as to the development of the integument in *Manis*, but merely the statement (p. 545): "The origin of the scales, which are strikingly large in the case of the small *Manidæ*, may well be explained by the fusion of several small scales. . . ." This mode of explanation is a personal one on the part of Römer. I have exerted myself to discover the development of the scales on his behalf, from their earliest appearance onwards, but have observed no trace whatever of a fusion of the scales. Since the investigation is a very easy one, I have no reason to deviate from what I saw and to adopt an explanation which is not based upon observation.

But also the manner of the occurrence of the scales in Mammals tells against the view that they are to be regarded as a new acquisition of a secondary character in connexion with the mode of life. A few examples may make this clear.

*Myrmecophaga tamandua*, whose climbing tail is but thinly clothed with hair, has the scales but little more strongly developed than the exclusively terrestrial *M. jubata*, whose tail is thickly clothed with bushy hair, and in spite of that bears scales. *Myrmecophaga (Cyclothurus) didactyla*, with an exclusively arboreal mode of life and a typical prehensile tail, has no trace of scales. Of *Ptilocercus* and *Tupaja*, which are the only arboreal Insectivores, *Ptilocercus* has, as shown by de Meijere, well-developed polygonal caudal scales, while *Tupaja*, with a precisely similar mode of life, has nothing of the kind. *Tarsius spectrum* of authors comprises, as I was able to prove\*, two species precisely similar in their mode of life. Of these the one, *Tarsius fuscomanus*, Fisch., has distinct scales on a hairy tail, while the almost bare tail of the other, *T. spectrum*, Pall., is entirely without them. Scales were found by de Meijere upon the thickly haired tails of *Petrogale penicillata* and *Macropus ruficollis*, while in the case

\* Max Weber, 'Zoolog. Ergebnisse einer Reise in Niederl. Ost-Indien,' Leiden, 1893, Bd. iii. p. 260.



of other species of *Macropus*, which use their tails in a precisely similar fashion, scales are wanting. What advantage does the short tail of *Perameles doreyanus* derive from its well-developed coat of scales, while the similarly constituted tails of *Perameles Gunni* and *P. obesula* are scaleless? The species of *Phalanger* with a typical prehensile tail are without a coat of scales, and the same applies to the prehensile tails of monkeys. The arboreal *Sciuridæ*, too, have scaleless tails. The large rows of scales on the ventral surface of the root of the tail of the *Anomaluridæ* are a specialization and a further development from small scales, which cover the entire tail.

Moreover, what is the nature of the adaptation that causes the extremities of many Marsupialia, Rodentia, and especially Insectivora to bear scales or indications of such?

The foregoing examples clearly illustrate the irregularity of the occurrence of scales even in the case of most closely allied species, as well as their independence of the mode of life of the animals. They become intelligible when we consider them from the point of view that scales are rudimentary structures, which have persisted in different degrees or in part already disappeared, and only in altogether isolated cases underwent further development in a specialized form (*Manidæ*, *Dasypodidæ*, *Castor*, *Anomalurus*). Römer, on the contrary, considers that the scales "are secondary phenomena of adaptation, which were acquired by true hair-bearing animals, since they were more advantageous to them for their mode of life, *e. g.* for the tail as a prehensile and supporting organ, than the less firm coat of hair."

On the other hand, Römer justly ascribes to me the view, that I held it to be improbable that the scales had developed as structures entirely new and without an inherited basis. In opposition to this Römer observes, "The inherited basis is, however, supplied in the wonderful capacity for differentiation possessed by the skin, which is indeed to be found in all groups of animals." What the respected author meant to convey by this somewhat formal paraphrase of the fact that the mammalian integument can actually produce scales, I was unable to quite understand. I found the greater difficulty in doing so since he goes on to state that "the scale-like coverings of Mammals, which develop in consequence of a capacity of the integument inherited from the Reptiles, and so to a certain extent are to be regarded as a case of 'throwing-back,' justify the conclusion that such a covering was formerly of general occurrence and clothed the entire body, or at least the dorsal parts thereof."

How great the agreement between us is may be gathered

from my previous words (*l. c.* p. 14) :—" I do not maintain that these scales, as they lie before us, are acquired from the Reptiles, but I regard as that which is inherited only the capacity of the caudal integument of *Anomalurus* to form such scales." And further on (p. 19) :—" We had come to the conclusion that the 'scales' of the Manidæ are structures which are to be derived from the scales of Reptiles. From our statement it will be clearly seen that we do not regard the two organs as completely homologous. The considerable difference between the horny scales of Reptiles and those of the Manidæ has indeed already been expressly pointed out. But we really believe that both had a common origin. . . ." When, therefore, Römer proceeds to declare that we must not, however, forget "that we here have not before us scales in their original form," I cannot apply the admonition to myself, if Römer by an "original" scale means a Reptilian one. Now, however, comes the difference, for Römer goes on to write—"but a secondary scale, which has developed anew upon true hair-bearing animals, for that is proved by the embryonic hairs of *Manis* \* and *Dasypus*, and is traceable to an adaptation of the skin to the mode of life." It is consequently assumed by Römer that Mammals, proceeding from scaly Reptiles, lost their coat of scales, developed hairs, and now could obtain scales once more only by adaptation to the mode of life, and therefore as a "secondary new acquisition."

In my opinion, however, the primitive Mammals, which developed from primitive, scaly, poikilothermic Reptiles, were clothed with scales. Behind these scales small and sparse hairs at first arose. Whether these were developed by modification from smaller scales or proceeded from nerve-end eminences which were situated between the scales I do not venture to decide.

With the production of the constant body-temperature and of vigorous metabolism, wherein influences of temperature must have been decisive, the hairy coat acquired a better development, since it protects the body against loss of heat by radiation and conduction. With this the integument had assumed its special Mammalian character, which also expressed itself in the scales, especially in their horny superstructure. Indeed I previously designated the difference between the Reptilian and Mammalian scales as one of the kind that belongs to the Reptilian and Mammalian integuments as such. With the increase in the number and size of the hairs, which conse-

\* The embryonic hairs of *Manis* only prove that the hairs are formed where they afterwards stand, consequently in always scanty numbers behind the scales.

quently owed their arrangement to the scales, the scales degenerated. In isolated cases only did they persist in a specialized form over the greater portion of the body (Manidæ, Dasypodidæ), otherwise usually upon the tail alone, and frequently also upon the extremities. Generally, however, they are already much reduced in the last-named region, and in the case of the majority of Mammals every trace of scales has disappeared. But very commonly the arrangement of the hairs has still remained, as though they yet stood behind scales. In this manner the hairs also point to the former presence of scales.

Contrary to my desire, this paper has assumed the appearance of a polemical character towards Römer's memoir. It seemed to me, however, to be of importance that now, when it is to be hoped that still further studies in a similar sense to that of Römer will advance the questions here touched upon, the different views should be accurately expressed and their mutual limits defined. By this means we shall attain a precise idea of the question at issue, which cannot fail to be advantageous.

Amsterdam, March 13, 1893.

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II.—*List of Insects collected by Miss Elizabeth Taylor in Western North America in the Summer of 1892.* By ARTHUR G. BUTLER, F.L.S., F.Z.S., &c., and W. F. KIRBY, F.L.S., F.E.S., &c.

### LEPIDOPTERA. By A. G. BUTLER.

MOST of the species recorded in the following list were obtained on the Slave River in the months of June and July. The collection is of interest as extending our knowledge of the range of species hitherto received from the Rocky Mountains, California, &c. Two species are described as new to science.

Of BUTTERFLIES twenty-three species are in the collection, of which ten belong to the Nymphalidæ, four to the Lycaenidæ, six to the Papilionidæ, and three to the Hesperiidæ.

#### 1. *Anosia plexippus*.

*Papilio plexippus*, Linnæus, Mus. Lud. Ulr. p. 262 (1764).

♀. Winnipeg, Manitoba, 11th September.